Size-Selective Predation in a Sea Anemone, Nudibranch, and Fish Food Chain

by

LARRY G. HARRIS

Zoology Department, University of New Hampshire, Durham, New Hampshire 03824, U.S.A.

Abstract.   A series of field and laboratory observations and experiments was used to determine whether size-selective predation by the aeolid nudibranch *Aeolidia papillosa* on its principal prey in the Gulf of Maine, the anemone *Metridium senile*, was a mechanism capable of producing the patterns of anemone population structure observed in subtidal habitats. Similar techniques were also used to test the hypothesis that size-selective predation by the wrasse *Tautogolabrus adspersus* on *A. papillosa* could account for the inverse relationship between aggregations of fish and the reduced presence of *A. papillosa* in association with *M. senile*. Field and laboratory studies showed that *A. papillosa* has a disproportionately negative impact on the smaller size classes of *M. senile*. An important factor in this preference was the size-related effectiveness of acontia extrusion as a defense by *M. senile* against *A. papillosa*. The results indicated that *M. senile* was a preferred prey for all life stages of *A. papillosa*, but that relative sizes of predator and prey were important factors. Field tests demonstrated that *T. adspersus* would eat *A. papillosa*, and the nudibranch is uncommon in habitats containing schools of the wrasse. Laboratory experiments showed that predation was size-selective, though investigative attacks were made on all size classes of nudibranchs offered. The results verify that size-selective predation by wrasses would explain the delayed appearance and reduced presence of *A. papillosa* with concentrations of *M. senile* in those habitats as compared to nearby areas without wrasses. Size-selective predation on the sea anemones would in turn provide a mechanism for the difference in sea anemone population structure, from scattered, large and solitary individuals to aggregated, small and clonal individuals, between areas with high and low nudibranch populations, respectively. It is proposed that indiscriminate investigative attacks by visual predators on the young stages of specialized grazing predators such as nudibranchs could be a significant factor influencing the co-evolution of predator-prey associations with sessile invertebrates, particularly in the tropics.

INTRODUCTION

PREDATION on nudibranch mollusks has been suggested but seldom documented, particularly for fish (see TODD, 1981). A similar lack of information is available on how nudibranchs impact prey populations, other than the studies by TODD (see review, 1981), and in these cases the emphasis is on the nudibranch predation. EDMUNDS (1966, 1974) and HARRIS (1973) have suggested that fish predation must be an important selective force, and TODD (1981) reported that wrasses readily consumed small nudibranchs and sacoglossans exposed when coral heads were overturned in the Red Sea. Similarly, several workers (EDMUNDS, 1966; HARRIS, 1973, 1976; SCHICK *et al.*, 1979) have hypothesized that the sea anemone-eating nudibranch *Aeolidia papillosa* (Linnaeus) may affect the pop-

ulation structure of its prey, but no effort has been made to document such an effect.

In the southern Gulf of Maine, the sea anemone *Metridium senile* is the only common species on hard substrates in the shallow subtidal (low water to −25 m). The principal predator is *Aeolidia papillosa* (CLARK, 1975). There is also one epibenthic picking fish, the wrasse *Tautogolabrus adspersus* (Walbaum, 1792). *Metridium senile* occurs in two conspicuous population structures: (1) scattered solitary individuals or small groups of moderate (> 40 mm column diameter) to large size individuals (SCHICK *et al.*, 1979) or (2) clones or aggregates of many individuals dominated by small (<20 mm column diameter) sea anemones (HOFFMANN, 1976). Populations of *A. papillosa* tend to occur more commonly with the dispersed

phase of *M. senile* than with the clonal form. *Tautogolabrus adspersus* is a conspicuous member of habitats containing clones of *M. senile*. Preliminary observations suggested that *T. adspersus* would eat *A. papillosa* and that the nudibranch had an effect on anemone population structure. The purpose of this report is to describe the results of observations and experiments investigating the effect of prey size on predation by the respective predators in this three-level predator-prey system.

MATERIALS AND METHODS

The majority of studies described here was conducted in subtidal locations in the Gulf of Maine in an area encompassing southern Maine and New Hampshire. Animals used in laboratory studies were maintained at 12°C in closed, recirculating seawater systems, housed in the Zoology Department at the University of New Hampshire.

Metridium senile

Sea anemone populations were sampled either with 0.1-m^2 quadrats placed randomly over sections of dense aggregations or by counting and measuring every sea anemone within a predetermined region when only scattered individuals were present. Sea anemones were measured to the nearest 5 mm in column diameter. More accurate measurement of *Metridium senile* is almost impossible due to the variability in pedal disc attachment configuration.

Information on asexual reproduction and survival was obtained by placing specimens of *Metridium senile* on granite blocks in Gosport Harbor, Isles of Shoals, at a depth of 10 m and monitoring them on a monthly basis from June 1977 to present. Wire cages (1.25-cm mesh) were used to exclude larger predators, particularly winter flounder, crabs, and lobsters. Individuals of *Aeolidia papillosa* were removed from the blocks as soon as they were observed.

Sea anemones for most laboratory experiments were collected from the undersides of floats at a boat marina in Beverly, Massachusetts. In this habitat there were extensive populations of *Metridium senile*, dominated by small individuals due to both asexual (pedal laceration) and sexual reproduction.

Nudibranchs for experiments were collected from aggregations of *Metridium senile*. Each individual was measured to the nearest mm for small (≤15 mm) individuals and 5 mm for animals greater than 15 mm. Nudibranchs were maintained in glass or plastic containers in which the water was changed daily. Pedal lacerates of *M. senile* were used as food.

Nudibranch Predation

To test for the influence of *Aeolidia papillosa* on *Metridium senile* population structure, groups of sea anemones were set up in four separate dishpans. The sea anemones ranged in number from 80 to 110 individuals and in each container the size range in column diameter was 2 to 75 mm. Once the sea anemones were attached, counted, and measured, five to ten *A. papillosa* were introduced into each container. The nudibranchs were allowed to feed for six weeks while the sea anemones were counted and measured on a weekly basis. A large sample of *M. senile* free in the same sea table served as the control. There was no mortality of sea anemones in the control tank during the experiment; *M. senile* of all sizes normally survive for months in the closed seawater system used.

The effect of prey size on *Aeolidia papillosa* survival and growth was tested by culturing small (3 to 12 mm) nudibranchs with either small (≤10 mm) or large (≥30 mm) sea anemones. Fifty nudibranchs in two tests (10 and 15 individuals per treatment, respectively) were cultured for one month in 40-cm glass stacking dishes. Water was changed every other day and small sea anemones were replaced as food when needed. Survival and growth rate were monitored.

Fish Predation

To test for possible wrasse predation on *Aeolidia papillosa*, nudibranchs were offered to individuals of *Tautogolabrus adspersus* in the field. To stimulate feeding behavior in two of the four tests, pieces of mussel (*Mytilus edulis*) were added to the area where the nudibranchs were placed. In one test, 26 nudibranchs were set out around sea anemones where no fish were in residence. A second set of 31 *A. papillosa* was taken to a small cave containing numerous *Metridium senile* and wrasses. The nudibranchs were placed on a rock among several anemones and set at the mouth of the cave. No bait was added and the fish were observed until all nudibranchs were consumed. The control nudibranchs were then collected. The fish behavior and any attacks were observed and recorded.

Once it was demonstrated that the wrasses did eat *Aeolidia papillosa*, a laboratory experiment was conducted to test for size-selective predation by wrasses on *A. papillosa*. Young *Tautogolabrus adspersus* (70 to 100 mm in length) were maintained in a shallow sea table. The fish were fed pieces of mussel tissue daily on a flat piece of slate to condition them to one specific feeding site. The experiment consisted of setting 10 small (1.5 to 15 mm) *A. papillosa* in a petri dish (6 cm in diameter) along with pieces of mussel tissue and placing it into the sea table on the slate. Ten replicates of this experiment were carried out. The behavior of the fish, number of attacks, and sizes of any nudibranchs consumed were recorded.

RESULTS AND OBSERVATIONS

Anemone Populations

Metridium senile is essentially the only sea anemone in the southern Gulf of Maine from the low tide mark to 25
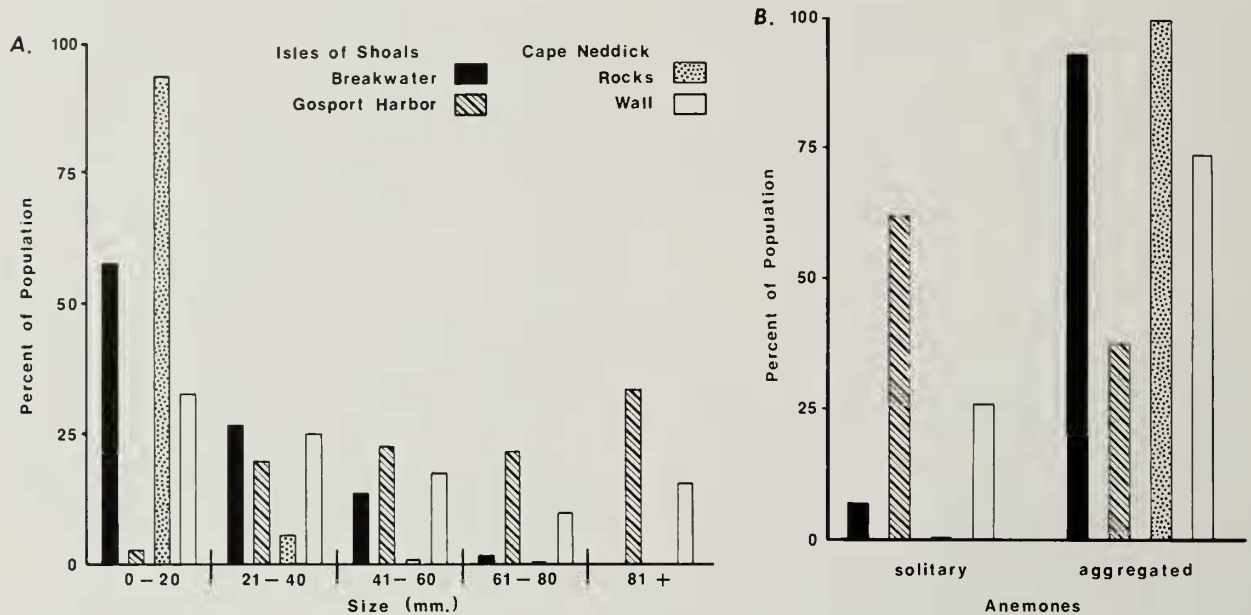
Figure 1

A comparison of the population structure of *Metridium senile* from two adjacent habitats at two locations in the Gulf of Maine. Sea anemone aggregations at the north Breakwater, Isles of Shoals, New Hampshire, and the rocks at Cape Neddick, Maine, occur in large numbers and were sampled using 0.1-m² quadrats. The populations of Gosport Harbor, Isles of Shoals, and the wall at Cape Neddick consist of scattered anemones on rock outcroppings with densities of less than 1/m², and sampling was done by measuring every anemone within a predetermined area. The two populations at each site are within 100 m of each other. Section A gives the population structure in percentage in each size class. Section B gives the population structure in terms of solitary individuals *versus* sea anemones aggregated into groups of two or more.

m in depth. Individuals may reach a column diameter of 30 cm, but few animals are greater than 10 cm in most habitats. The population structure varies considerably with the habitat (HOFFMANN, 1976; SCHICK *et al.*, 1979). Figure 1 illustrates the two major patterns of *M. senile* population structure in the Gulf of Maine. The sea anemone population structures at the sites given in Figure 1 have remained stable for the 16 years I have been working in these habitats, and the same patterns have been observed in numerous other locations from Eastport, Maine, to Boston, Massachusetts. Large aggregations of *M. senile* occur in many fouling communities, on large subtidal, vertical, or undercut rock faces and breakwaters, and on large boulders at depths greater than 20 m. These aggregations typically contain a high percentage (>50%) of small sea anemones less than 20 mm in column diameter—the products of asexual and sexual reproduction.

Scattered on hard substrates in almost any habitat are populations of *Metridium senile* occurring in small clumps of less than 10 individuals and primarily as solitary individuals. A majority of the sea anemones in the dispersed populations is larger in size (≥50 mm).

Asexual reproduction occurs throughout the year, but it reaches a peak in early summer, beginning shortly after the barnacle *Balanus balanoides* (L.) completes its plank-

tonic phase. The stomach contents of *Metridium senile* are dominated by *B. balanoides* cyprids at this time. Sexual reproduction as indicated by the release of planulae, and the appearance of small sea anemones occurs in June and early July (unpublished observations). Therefore, by late summer, small sea anemones (≤10 mm) are common in all habitats.

In mid-July, small (<5 mm) *Aeolidia papillosa* begin to appear in large numbers wherever *Metridium senile* is found and this pattern continues into November (HARRIS, 1973). These small nudibranchs remain in close proximity (<5 cm) to sea anemones. As is illustrated in Figure 2, higher numbers of nudibranchs are associated with the scattered sea anemones. Also, the early appearance of large *A. papillosa* in association with the dispersed sea anemones suggests higher survival of nudibranchs settling in these habitats; as is seen in Figure 2B, there was a large population of nudibranchs already established on the wall at Cape Neddick, before any were found among the sea anemones at the rock site. *Aeolidia papillosa* tends to be cryptic in coloration and nocturnal in activity, but it seldom moves far from sea anemones, so it is easy to observe on large rock surfaces where *M. senile* is most common in subtidal habitats.

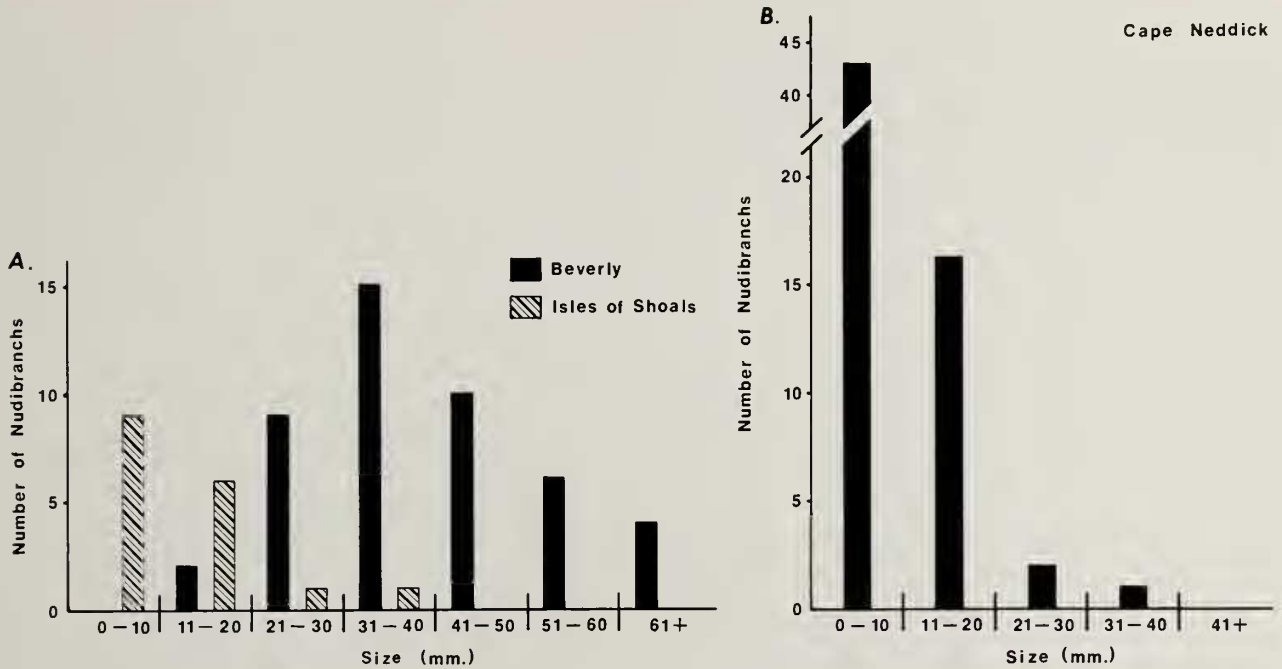The nudibranchs that occur with aggregated *Metridium*

Figure 2

A comparison of numbers and size distributions of *Aeolidia papillosa* collected from sites where anemones were dispersed or primarily aggregated into clones. A. The nudibranchs from under and around small rocks below floats in Beverly, Massachusetts, took 5 min to collect; there were also numerous egg masses present. The *A. papillosa* collected on the breakwater at the Isles of Shoals during the same week in March 1978, required 45 min of intensive searching and no egg masses were seen (chi square, $P < 0.01$). B. Approximately 30 min were spent hunting for nudibranchs at each site as part of a single SCUBA dive at Cape Neddick, Maine (October 1978). No nudibranchs were found at the rocks site (see Figure 1A) where wrasses are common, but *A. papillosa* were common around sea anemones at the wall site.

senile tend to be fewer in number and to appear later in the fall. This suggests either differential survival or differential settlement depending on the habitat. One of the most conspicuous differences between the habitats where scattered *versus* aggregated *M. senile* are found is the presence of the wrasse *Tautogolabrus adspersus*. *Tautogolabrus adspersus* tends to aggregate in habitats where there is cover in the form of crevices and caves. It is on the vertical and undercut walls of these refuges that *M. senile* occurs in aggregated populations. The delayed appearance of *Aeolidia papillosa* in these areas correlates with the fall disappearance of *T. adspersus* as it migrates to deeper water or hibernates (GREEN & FARWELL, 1972). Nudibranchs were also found with sea anemones on the caged granite blocks (Table 1) well before any were observed with *M. senile* on nearby rocks containing resident populations of wrasses.

Aeolidia papillosa remains common through the winter. Reproduction begins in the southern Gulf of Maine in February and peaks in May, though it is still possible to find a few large reproducing animals into July. There is much variation in this cycle, but the general pattern has

been consistent from the fall of 1969 to the summer of 1985.

In scattered sea anemone populations, survival of small sea anemones produced each summer is low and coincides with the presence of numerous *Aeolidia papillosa* in these habitats through the late summer and fall. The results of caging experiments given in Table 1 illustrate the pattern of asexual reproduction by *Metridium senile*, followed by the disappearance of young sea anemones associated with the appearance of nudibranchs. These observations suggest that *A. papillosa* is having a disproportionate impact on the young sea anemones (HARRIS, 1976). This hypothesis was tested in a laboratory experiment (Figure 3). The differential predation by *A. papillosa* on sea anemones of smaller column diameter is clearly documented. There was no mortality of sea anemones in either the experimental or the control populations from factors other than feeding by nudibranchs, which was readily observed. No sea anemones under 15 mm remained in any of the experimental containers. The patterns documented in Figure 3 and Table 1 have been consistently observed when maintaining *A. papillosa* in the laboratory. Over a period

Table 1

Summary of field data illustrating the impact of *Aeolidia papillosa* predation on *Metridium senile* population structure. Sea anemones (30–80-mm column diameter) were placed on granite blocks on a sand substrate in Gosport Harbor, Isles of Shoals, in June 1977, and then monitored monthly. The blocks were caged to exclude large predators. Nudibranchs were removed when encountered. The data for sea anemones on four blocks are given for two summers (1978 and 1979). Ms = adult *M. senile*; pl = pedal lacerates <10 mm; Ap = *A. papillosa*.

Block no.	June 1978	August 1978		September 1978		March 1979	July 1979		September 1979	
5	5 Ms	4 Ms	4 pl	4 Ms 1 Ap	0 pl (25 mm)	4 Ms	4 Ms	30 pl	0 Ms	
6	1 Ms	1 Ms	14 pl	1 Ms 1 Ap	0 pl (25 mm)	1 Ms	1 Ms	0 pl	0 Ms	
7	5 Ms	5 Ms 1 Ap	31 pl (6 mm)	5 Ms 5 Ap	0 pl (7, 15, 14, 5, 10 mm)	5 Ms	5 Ms 1 Ap	51 pl (2 mm)	1 Ms 6 Ap	(8, 12, 22, 20, 20, 20 mm)
8	4 Ms	4 Ms 1 Ap	0 pl (40 mm)	4 Ms			3 Ms	3 Ms 11 pl	2 Ms 2 Ap	(30, 12 mm)
Totals	15 Ms 0 pl 0 Ap	14 Ms 49 pl 2 Ap		14 Ms 0 pl 7 Ap		13 Ms 0 pl 0 Ap	13 Ms 92 pl 1 Ap		3 Ms 0 pl 8 Ap	

of time, all sea anemones will be consumed except for a few large individuals. These larger sea anemones will be attacked and suffer some tissue loss, but they are able to survive repeated attacks and often to repel the nudibranch.

The reason for the preference of *Aeolidia papillosa* for small sea anemones is obvious. *Metridium senile* releases nematocyst-laden acontia (string-like extensions of the mesenterial filaments) through small pores (cinclides) in the column. If these acontia become tangled in the cerata of the nudibranch, the massive discharge of nematocysts can kill the nudibranch. This defensive mechanism appears to be (1) size-related and (2) more effective in the quiet conditions in the laboratory than in the much more complex environment of the field. The results in each of the two culturing experiments were not quite significant, although the combined results are certainly suggestive of the advantages of attacking small *Metridium*: 19 out of 25 survivors and a 4.5% increase in length per day for nudibranchs eating small sea anemones, and 9 out of 25 survivors and a mean growth rate of 2.42% increase in length per day for those fed large sea anemones. Not only was survival and growth rate higher for the animals fed small sea anemones, but only those nudibranchs forced to eat larger sea anemones suffered tissue damage or mortality from acontia—7 animals out of 25. It is quite common for small nudibranchs to stop eating and slowly starve to death when offered only larger *M. senile*. The same pattern of poor growth and survival of small *A. papillosa* cultured with large *M. senile* has been observed in studies conducted at Hopkins Marine Station in Pacific Grove, California, using animals collected in Monterey Bay (un-

published observations). Freshly killed *A. papillosa* wrapped in acontia have also been found in the field.

Fish predation on *Aeolidia papillosa* was verified first in the field by offering nudibranchs to wrasses in three habitats with positive results in each case. The observations indicated that size was an important component of this predation. The first set of tests illustrates this point. Two *A. papillosa* 20 mm in length were collected from the wall, Cape Neddick (Figures 1, 2), and taken to the rock site where numerous *Tautogolabrus adspersus* were aggregated. One nudibranch was tossed into the water column. A 15-cm long fish took it into its mouth and spat it out. A second wrasse, 25 cm in length, engulfed the nudibranch, spat it out, engulfed and spat it out again, and then swallowed it. The second *A. papillosa* was also eaten by this same wrasse after rejecting it three times. In fact, it was only eaten when a second fish came up to investigate. The test was repeated using a specimen of the aeolid *Coryphella verrucosa* (Sars) also 20 mm in length. Several fish looked closely at it and the wrasse that had eaten the *A. papillosa* tasted it once and would not go near it again. *Coryphella verrucosa* has bright red cerata with contrasting white markings, whereas *A. papillosa* is mottled brown and pale white. *Coryphella verrucosa* is conspicuously active during the day, whereas *A. papillosa* tends to be nocturnal and cryptically positioned during the day, although still visible to divers and fish on open surfaces. Wrasses offered *C. verrucosa* in the laboratory consistently rejected them. In both of the other field tests individuals of *A. papillosa* were eaten and it was always by the largest wrasses present.

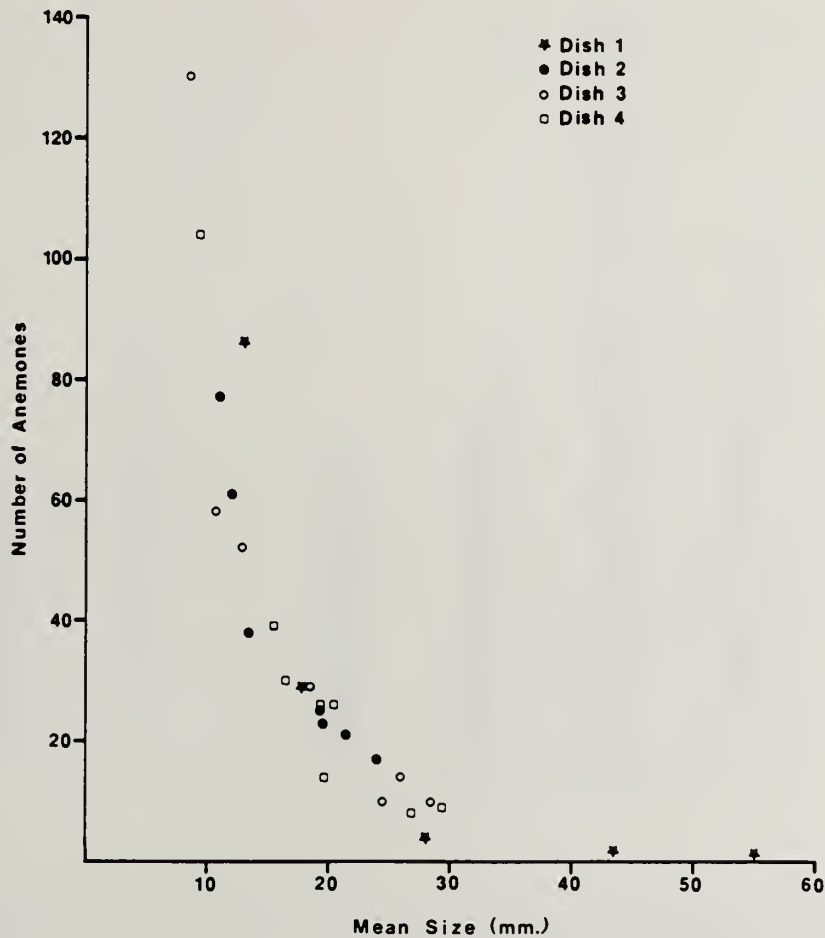One field experiment was also conducted to further de-

Figure 3

Summary of four feeding experiments in which individuals of *Aeolidia papillosa* were placed in containers with individuals of *Metridium senile* ranging in column diameter from 2 to 75 mm. The nudibranchs were allowed to feed for 6 wk and changes in the number and mean column diameter of all sea anemones were recorded. There was no mortality among the 300+ sea anemones serving as a control held in the same sea table with the experimental treatments. (Spearman-rank correlation coefficient <0.05 for dish one and <0.1 for dishes 2–4.)

termine whether *Tautogolabrus adspersus* predation could explain the lack of *Aeolidia papillosa* among *Metridium senile* where wrasses are common. The 26 nudibranchs placed among sea anemones on the wall at Cape Neddick (see Figure 1A) remained in place for about 3 h, and all individuals were retrieved. Thirty-one *A. papillosa* (1.5 to 2.5 cm in length) were taken to a cave at the rock site at Cape Neddick (Figure 1A) where more than 15 *T. adspersus* (15 to more than 30 cm in length) were in residence. A rock from the cave was retrieved and the nudibranchs were placed on the rock among several individuals of *M. senile*. There was a surge and 15 nudibranchs were lost in the transfer to the rock. The rock with the remaining 16 *A. papillosa* was placed just inside the cave mouth. No bait was used.

After about 3 min, individual fish began to swim up to the rock and investigate the surface, as they were doing to other rock surfaces in the vicinity of the cave. A number of fish bit at objects on the rock. Eleven nudibranchs were seen being engulfed and all 16 *Aeolidia papillosa* were removed in 17 min. None of the observed fish remained at the rock to attack several nudibranchs consecutively, but each fish tended to spend a short time at the rock and then move on. Several fish did return to the rock more than once during the period of observation. Fish often mouthed the nudibranchs before swallowing them, but in only two cases were nudibranchs spit out and then engulfed a second time. None of the fish rejected an engulfed *A. papillosa.*

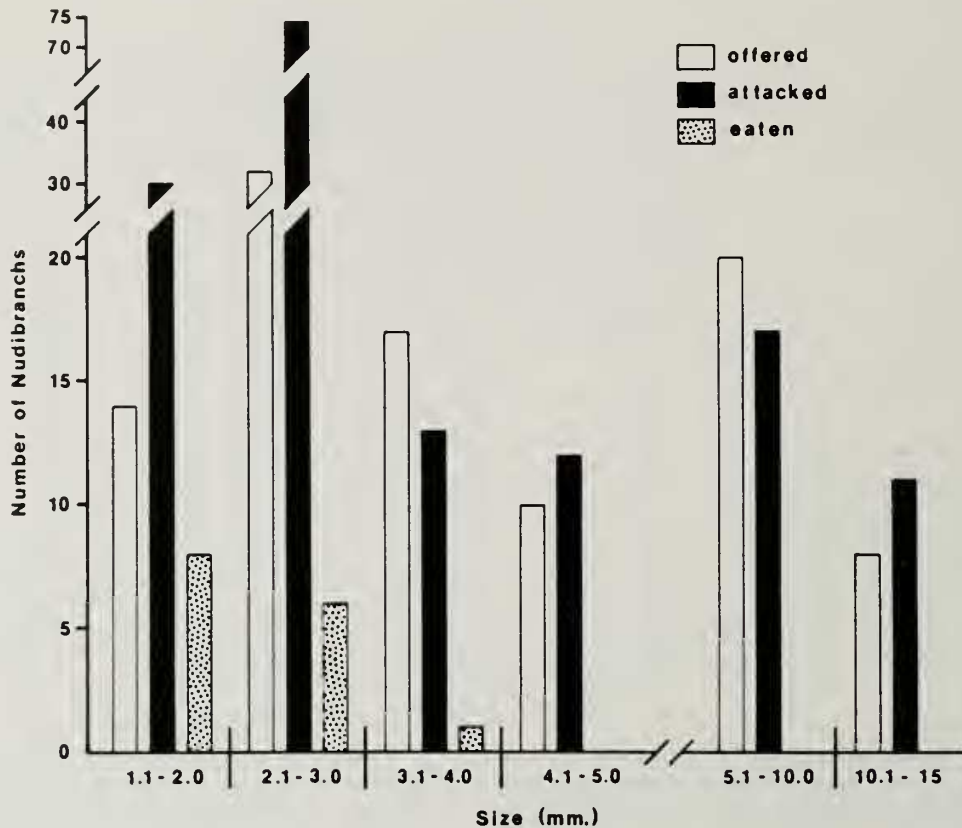Large (>30 cm body length) winter flounder forage on

Figure 4

Summary of feeding experiments in which 10 replicates of *Aeolidia papillosa,* along with small pieces of mussel tissue, were offered to a group of *Tautogolabrus adspersus* to test for size-selective predation. The total number of nudibranchs used, number of attacks, and number eaten are presented by mm size class. A nudibranch was often attacked more than once by one or more fish before it was rejected or eaten. All three categories were statistically different, $P < 0.01$, using the Kolmogorov-Smirnov test for goodness of fit.

rocky substrates and eat a variety of sessile algae and invertebrates including *Metridium senile*. On one occasion two large (about 50 mm) *Aeolidia papillosa* were found in a flounder stomach that also contained numerous anemones. Starved lobsters and spider crabs will eat *A. papillosa* after removing the cerata. However, the process is a slow one and the crustaceans will readily drop the nudibranchs if offered other food. *Aeolidia papillosa* is able to regenerate lost cerata and it is common to find large nudibranchs in the field regenerating cerata. Neither *Cancer borealis* (Stimpson), *Cancer irroratus* (Say), nor any asteroid species has been observed to eat *A. papillosa*.

The laboratory experiment testing fish predation on *Aeolidia papillosa* is summarized in Figure 4. The results clearly show that fish did selectively consume the smallest nudibranchs present, although they made investigative attacks on all sizes. Often a nudibranch that was eaten would be engulfed and rejected several times by more than one fish before it was swallowed; this was particularly true for the 2.1–3.0-mm size class. Many of the fish made

exaggerated ventilating movements after mouthing a nudibranch as if the lining of the mouth were irritated. *Aeolidia papillosa* releases both nematocysts and secretions from epidermal glands in the cerata when disturbed. Future experiments are planned to determine whether nematocysts are affecting the lining of the fish's mouth.

The fish used in the laboratory experiments became wary of attacking nudibranchs after the sixth trial. In the first six trials there was a mean of 22 investigative attacks per trial and only 7.5 attacks per trial for the last four. The fish became much more selective in picking pieces of mussel tissue and avoiding nudibranchs, which they visually investigated. The behavior of the fish suggested that they were learning from the larger nudibranchs in the dish and then avoiding the smaller individuals; no nudibranchs were consumed in the last two trials.

The results from one additional trial are suggestive of the mechanism involved in the avoidance, but the lack of small nudibranchs precluded further experiments at the time. To test the hypothesis that the wrasses were learning

from the larger nudibranchs, the following sequence was tested in a 30-min period:

one 2-mm *Aeolidia papillosa* was introduced along with food—it was eaten; a second 2-mm nudibranch was added without food—it was attacked and eaten;

the normal complement of 10 nudibranchs of various sizes (2–12 mm) plus food was added—there were nine investigative attacks, but no nudibranchs were eaten;

one 2-mm nudibranch plus food was introduced—the fish looked at it and ate the food, but would not touch the nudibranch.

DISCUSSION

This report concerns predation as a mechanism regulating nudibranch and sea anemone populations in the Gulf of Maine. Although the evidence described suggests that predation may be responsible for the observed population patterns, there are certainly other abiotic and biotic factors that influence the population structure and distribution of the species in question. Factors such as currents, food availability, competition, and disturbances other than predation almost certainly play a role in determining the population patterns of sea anemones and their nudibranch predators. HARRIS & IRONS (1982) suggested that population and community patterns are the result of a suite of factors that interact synergistically to produce the observed results. Therefore, the emphasis on predation here assumes that this factor is only one of several that interact to determine population patterns.

The observations and experiments described herein show that the wrasse *Tautogolabrus adspersus* does prey on the nudibranch *Aeolidia papillosa,* and laboratory experiments suggest that this predation is most intense on smaller nudibranchs. There is also evidence from both the field and laboratory that *A. papillosa* is a size-selective predator on its principal prey, the sea anemone *Metridium senile.* Clonal aggregations of sea anemones are typically found in habitats also containing schools of wrasses; in these conditions the appearance of nudibranchs is delayed and their numbers lower than in adjacent habitats where fish are scarce and sea anemones are large and scattered.

Metridium senile is an effective space competitor in fouling communities capable of outcompeting most other sessile invertebrates (HARRIS & IRONS, 1982) and dominating large areas of primary space (HOFFMANN, 1976; PURCELL, 1977). SCHICK *et al.* (1979) and I (HARRIS, 1973, 1976) have suggested that predation by *Aeolidia papillosa* can alter the population structure of *M. senile* by consuming small individuals.

The results of observations (Table 1) and experiments (Figure 3) verify that this hypothesis is at least one mechanism capable of producing the patterns observed. R. T. Paine (personal communication) found that clones of *Metridium senile* protected by cages suffered size-selective mortality relating to the presence of *Aeolidia papillosa,* re-

sulting in the disappearance of all smaller sea anemones. I recorded a similar direct relationship between *M. senile* mean size and *A. papillosa* density in comparing sea anemone populations on the pilings of the Commercial Wharf in Monterey Bay and on rock piles below the pilings, where *A. papillosa* commonly hide (1973, 1976, unpublished observations).

The defensive response of *Metridium senile* has been described previously (HARRIS, 1973; EDMUNDS *et al.,* 1976). The effectiveness of acontia extrusion is suggested by growth experiments, but even here it is relative size that is important. Numerous observations over the last 16 yr indicate that acontia extrusion is most effective as a defense under laboratory conditions where there is no water movement or structure to interfere with the acontia. I have often observed *Aeolidia papillosa* attacking large *M. senile* in the field with acontia drifting back and forth in the surge or hung up on nearby sea urchin spines, algae, or hydroids. This increased effectiveness in the laboratory is almost the exact opposite of the situation described for the west coast sea anemone *Anthopleura elegantissima* (Brandt), in which the sea anemone is almost totally defenseless against *A. papillosa* under laboratory conditions (HARRIS & HOWE, 1979).

The selection for small *Metridium senile* by *Aeolidia papillosa* has another implication relative to prey preference by this nudibranch. WATERS (1973), HARRIS (1973), and EDMUNDS *et al.* (1975) have reported from laboratory studies that *M. senile* was one of the least preferred prey of *A. papillosa*. However, in the field, *A. papillosa* is typically found associated with *M. senile,* even where more preferred prey are available. This led to the hypothesis that settling veligers of *A. papillosa* had a different preference hierarchy than the adults (HARRIS & HOWE, 1979). The previous studies had all used large *M. senile* which, as demonstrated here, are most effective in repelling attacks in the laboratory. HARRIS & DUFFY (1980) found that *A. papillosa* fed small *M. senile* and *Anthopleura elegantissima* showed no preference for either species in olfactometer tests, but switched to a strong selection for *A. elegantissima* when offered only large *M. senile* in combination with *A. elegantissima*. The results reported here suggest that *M. senile* is a preferred prey of *A. papillosa* throughout their overlapping ranges in the Atlantic and Pacific oceans, but that size is an important influencing factor.

Differential mortality on the young stages of many groups of plants and animals is a well documented phenomenon (DEEVEY, 1947; MECK, 1966; THORSON, 1966; JANZEN, 1970; CONNELL, 1970; DAYTON, 1971; SUTHERLAND, 1974; PAINE, 1976; RUSS, 1980). Conversely, large size as a defensive mechanism is also well known (MECK, 1966; CONNELL, 1970; JANZEN, 1970; DAYTON, 1971; PAINE, 1974, 1976). SEBENS (1979) has suggested that the trend to larger sizes in the lower intertidal in the anemone *Anthopleura elegantissima* is due to energetic considerations—the longer submersion time allows greater feeding

time and therefore greater size. A complementary explanation for the large size of lower intertidal, as well as subtidal, sea anemones is defense from predators (HARRIS & HOWE, 1979). This appears to be an important selective force for *Metridium senile* in the Gulf of Maine. *Aeolidia papillosa* is also a major sea anemone predator on the Pacific Coast of North America, but it is not as conspicuous as the seastar *Dermasterias imbricata* (Grube) which also eats sea anemones (MAUZEY *et al.*, 1968). *Dermasterias imbricata* grows to a much larger size than *Aeolidia papillosa* and kills anemones by covering them in folds of its cardiac stomach. Field and laboratory observations indicate that *D. imbricata* is size-limited in its ability to attack anemones (Harris, unpublished observations) and this starfish may exert a greater selective force on the size and habitat selection of subtidal sea anemones on the West Coast of North America than *A. papillosa*.

Fish predation on the young stages of fouling community organisms has been shown by SUTHERLAND (1974), DAY (1977), and RUSS (1980). The results of this predation were to alter community structure. MONTGOMERY *et al.* (1980) have documented size-selective grazing on brown algal species that are avoided as adults by surgeon fishes in the Gulf of California. EDMUNDS (1966) concluded that fish predation must be an important selective factor in the development of aeolid nudibranch defensive mechanisms. I (HARRIS, 1973) proposed that investigative attacks by fish on the young stages of two coral-eating nudibranchs of the genus *Phestilla* (Bergh) was an important selective force and source of mortality for these species. Both *Phestilla* species are similar to *Aeolidia papillosa* in that they are cryptic, nocturnal, and aggregate. The results of this study (Figure 4) represent the first documentation of size-selective predation by fish on nudibranchs. The behavior observed during these experiments, as well as previous studies (HARRIS, 1973; TODD, 1981), strongly suggests that the mechanism involved is a combination of image recognition coupled with a concentration level of defensive secretions and (or) nematocysts. *Tautogolabrus adspersus* is an epibenthic predator that visually selects small prey items, sessile and motile, from the substrate (CHAO, 1973; SHUMWAY & STICKNEY, 1975; HARRIS & IRONS, 1982). This wrasse plays a role in the Gulf of Maine similar to that of the great diversity of more specialized epibenthic pickers so conspicuous in the tropics (BAKUS, 1964, 1966; RANDALL, 1967; RANDALL & BROCK, 1960; RANDALL & HARTMAN, 1968; SALE, 1980; CHOAT, 1982). It appears that individuals of *T. adspersus* do not recognize as distasteful small specimens of *A. papillosa*, which are cryptically colored and inactive during the day. This suggests that below some relative size the nudibranchs are neither distinctive enough nor distasteful enough for avoidance learning to take place (WICKLER, 1968; EDMUNDS, 1974). Larger specimens of *A. papillosa* do appear to achieve a size at which *T. adspersus* learns to avoid them. If the observations suggesting *T. adspersus* learns to recognize small *A. papillosa* as distasteful from

encounters with larger individuals are valid, then the strong tendency for *A. papillosa* to aggregate would have a defensive advantage as well as the obvious one for successful reproduction.

The size at which wrasses avoid *Aeolidia papillosa* is relative. Although 10-cm long wrasses did not eat any nudibranchs greater than 3.5 mm, a 25-cm wrasse ate two 20-mm *Aeolidia papillosa*. *Tautogolabrus adspersus* seldom reaches much more than 35 cm in length, but *A. papillosa* grows to over 80 mm and does appear to have a refuge in size, at least from wrasse predation. Also, *A. papillosa* is cryptic and uncommon in most habitats, so it is unlikely that *T. adspersus* would encounter enough individuals to develop the obvious avoidance response shown to the common and brightly colored (red and white) *Coryphella* spp.

Tautogolabrus adspersus and numerous tropical species tested refused to eat large nudibranchs (HARRIS, 1973; EDMUNDS, 1974), which have an impressive array of defensive secretions and in some cases nematocysts (EDMUNDS, 1966, 1974). However, fish that feed by selecting items from epibenthic surfaces make many investigative attacks, rejecting the distasteful or inedible objects. It is not necessary for visual pickers to actively seek out the young stages of nudibranchs to have a negative impact on their distribution—indiscriminate investigative attacks should have the same adverse influence on the young stages of a species. It is therefore proposed that this mechanism of indiscriminate investigative attacks on the young stages of specialized grazers (*i.e.*, opisthobranchs) on sessile organisms may be a significant selective factor influencing the co-evolution of specialized predator-prey associations. The result of such selection would be to relegate most associations to cryptic habitats, which is where most tropical opisthobranchs are found. Conversely, sessile forms adapted to occupy open surfaces would be relatively free of specialized grazers, but must then emphasize competitive mechanisms and strategies to avoid generalized grazers (see WELLS *et al.*, 1964).

ACKNOWLEDGMENTS

LITERATURE CITED

BAKUS, G. J. 1964. The effects of fish-grazing on invertebrate evolution in shallow tropical waters. Allan Hancock Foundation Publications, No. 27:1–29.

BAKUS, G. J. 1966. Some relationships of fishes to benthic organisms on coral reefs. Nature 210:280–284.

CHAO, L. N. 1973. Digestive system and feeding habits of the cunner, *Tautogolabrus adspersus*, a stomachless fish. Fish. Bull. 71:565–586.

CHOAT, J. H. 1982. Fish feeding and the structure of benthic

communities in temperate waters. Ann. Rev. Ecol. Syst. 13: 423–449.

CLARK, K. B. 1975. Nudibranch life cycles in the northwest Atlantic and their relationship to the ecology of fouling communities. Helgol. Wissenschaft. Meeres. 27:28–69.

CONNELL, J. H. 1970. A predator-prey system in the marine intertidal region. I. Balanus glandula and several predatory species of Thais. Ecol. Monogr. 40:49–78.

DAY, R. W. 1977. Two contrasting effects of predation on species richness in coral reef habitats. Mar. Biol. 44:1–5.

DAYTON, P. K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecol. Monogr. 41: 351–389.

DEEVEY, E. S., JR. 1947. Life tables for natural populations of animals. Quart. Rev. Biol. 22:283–314.

EDMUNDS, M. 1966. Protective mechanisms in the Eolidacea (Mollusca, Nudibranchia). J. Linn. Soc. Lond., Zool. 46: 46–71.

EDMUNDS, M. 1974. Defense in animals. Longman, Inc.: New York. 357 pp.

EDMUNDS, M., G. W. POTTS, R. C. SWINFIN & V. L. WATERS. 1975. The feeding preferences of Aeolidia papillosa (L.) (Mollusca, Nudibranchia). J. Mar. Biol. Assoc. U.K. 54: 939–947.

EDMUNDS, M., G. W. POTTS, R. C. SWINFIN & V. L. WATERS. 1976. Defensive behavior of sea anemones in response to predation by the opisthobranch mollusc Aeolidia papillosa (L.). J. Mar. Biol. Assoc. U.K. 56:65–83.

GREEN, J. M. & M. FARWELL. 1972. Winter habits of the cunner Tautogolabrus adspersus (Walbaum, 1792), in Newfoundland. Can. J. Zool. 49:1497–1499.

HARRIS, L. G. 1973. Nudibranch associations. Pp. 213–315. In: T. C. Cheng (ed.), Current topics in comparative pathobiology. Vol. II. Academic Press: Baltimore, MD.

HARRIS, L. G. 1976. Comparative ecological studies on the nudibranch Aeolidia papillosa and its anemone prey Metridium senile along the Atlantic and the Pacific coasts of the United States. J. Moll. Stud. 42:301 (abstract).

HARRIS, L. G. & S. J. DUFFY. 1980. The influence of prey size on the preference hierarchy of the nudibranch Aeolidia papillosa (L.). Amer. Zool. 20:1087 (abstract).

HARRIS, L. G. & N. R. HOWE. 1979. An analysis of the defensive mechanisms observed in the anemone Anthopleura elegantissima in response to its nudibranch predator Aeolidia papillosa. Biol. Bull. 157:138–152.

HARRIS, L. G. & K. P. IRONS. 1982. Substrate angle and predation as determinants in fouling community succession. Pp. 131–174. In: J. Cairns (ed.), Artificial substrates. Ann Arbor Science Publishers, Inc.: Ann Arbor.

HOFFMANN, R. J. 1976. Genetics and asexual reproduction of the sea anemone Metridium senile. Biol. Bull. 151:478–488.

JANZEN, D. H. 1970. Herbivores and the number of tree species in tropical forests. Amer. Natur. 104:501–528.

MAUZEY, K. P., C. BIRKELAND & P. K. DAYTON. 1968. Feeding behaviour of asteroids and escape responses of their prey in the Puget Sound region. Ecology 49:603–619.

MECK, L. D. 1966. The wolves of Isle Royale. Fauna of the National Parks of the United States, Fauna Series 7. U.S. Government Printing Office: Washington, D.C. 210 pp.

MONTGOMERY, W. L., T. GERRODETTE & L. D. MARSHALL. 1980. Effects of grazing by the yellowtail surgeonfish, Prionurus punctatus, on algal communities in the Gulf of California, Mexico. Bull. Mar. Sci. 30:901–908.

PAINE, R. T. 1974. Intertidal community structure. Experimental studies on the relationship between a dominant competitor and its principal predator. Oecologia 15:93–120.

PAINE, R. T. 1976. Size-limited predation: an observational and experimental approach with the Mytilus-Pisaster interaction. Ecology 57:858–873.

PURCELL, J. E. 1977. Aggressive function and induced development of catch tentacles in the sea anemone Metridium senile (Coelenterata, Actiniaria). Biol. Bull. 153:355–368.

RANDALL, J. E. 1967. Food habits of reef fishes of the West Indies. Stud. Trop. Oceanogr. (Miami) 5:665–847.

RANDALL, J. E. & V. E. BROCK. 1960. Observations on the ecology of epinepheline and lutjanid fishes of the Society Islands, with emphasis on food habits. Trans. Amer. Fish. Soc. 89:9–16.

RANDALL, J. E. & W. D. HARTMAN. 1968. Sponge-feeding fishes of the West Indies. Mar. Biol. 1:216–225.

RUSS, G. 1980. Effects of predation by fishes, competition, and structural complexity of the substratum on the establishment of a marine epifaunal community. J. Exp. Mar. Biol. Ecol. 42:55–69.

SALE, P. F. 1980. The ecology of fishes on coral reefs. Oceanogr. Mar. Biol. Ann. Rev. 18:367–421.

SCHICK, J. M., R. J. HOFFMANN & A. N. LAMB. 1979. Asexual reproduction, population structure, and genotype-environment interactions in sea anemones. Amer. Zool. 19:699–713.

SEBENS, K. P. 1979. The energetics of asexual reproduction and colony formation in benthic marine invertebrates. Amer. Zool. 19:683–697.

SHUMWAY, S. E. & R. R. STICKNEY. 1975. Notes on the biology and food habits of the cunner. N.Y. Fish and Game J. 22:71–79.

SIMENSTAD, C. A., J. A. ESTES & K. W. KENYON. 1978. Aleuts, sea otters, and alternate stable-state communities. Science 200:403–411.

SUTHERLAND, J. P. 1974. Multiple stable points in natural communities. Amer. Natur. 108:859–873.

THORSON, G. 1966. Some factors influencing the recruitment and establishment of marine benthic communities. Neth. J. Sea Res. 3:267–293.

TODD, C. D. 1981. The ecology of nudibranch molluscs. Oceanogr. Mar. Biol. Ann. Rev. 19:235–380.

WATERS, V. L. 1973. Food-preference of the nudibranch Aeolidia papillosa, and the effect of the defenses of the prey on predation. Veliger 15:174–192.

WELLS, H. W., M. J. WELLS & I. E. GRAY. 1964. Ecology of sponges in Hatteras Harbor, North Carolina. Ecology 45: 752–767.

WICKLER, W. 1968. Mimicry in plants and animals. McGraw-Hill Book Company: New York. 255 pp.